



# Modeling potential outcomes of fire and fuel management scenarios on the structure of forested habitats in northeast Oregon, USA

Barbara C. Wales<sup>a,\*</sup>, Lowell H. Suring<sup>b</sup>, Miles A. Hemstrom<sup>c</sup>

<sup>a</sup> USDA Forest Service, Pacific Northwest Research Station, Forestry and Range Sciences Laboratory, 1401 Gekeler Lane, La Grande, OR 97850, USA

<sup>b</sup> USDA Forest Service, Terrestrial Wildlife Ecology Unit, Aquatic Sciences Laboratory, 322 East Front Street, Suite 401, Boise, ID 83702, USA

<sup>c</sup> USDA Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 620 SW Main, Suite 400, Portland, OR 97205, USA

## Abstract

Thinning and prescribed fire are being used extensively across the interior western United States to reduce the risk of large, severe wildfires. However, the full ecological consequences of implementing these management practices on the landscape have not been completely evaluated. We projected future vegetation trends resulting from four management scenarios and compared vegetation trends against the natural range of variability (NRV) using a state and transition model that included natural disturbances (e.g., wildfires, insect outbreaks) on a study area in northeast Oregon. We tracked the area of forests with large trees to assess potential trends of habitat for wildlife species closely associated with these forest structures and evaluated land allocations that restricted management practices on national forests (i.e., riparian and old-growth forests). We also specifically analyzed habitat available for Canada lynx (*Lynx canadensis*), a species listed as threatened under the USA Endangered Species Act. This included an evaluation of implementing and not implementing current management practices designed to protect Canada lynx habitat. We found that the area of forests in large-diameter ( $\geq 52.5$  cm) trees is currently well below the estimated NRV, and that it might take  $>100$  years to return to more natural levels regardless of the management scenario implemented. In addition, fuels management activities (i.e., thinning, prescribed fire) resulted in total area of closed-canopy large- and medium-diameter ( $\geq 40$  cm) forests well below that predicted under a natural disturbance regime, particularly in cool-moist and cold forests.

© 2006 Elsevier B.V. All rights reserved.

**Keywords:** Forest restoration; Fuels management; Habitat modeling; *Lynx canadensis*; Interior Northwest Landscape Analysis System (INLAS); Wildlife habitat

## 1. Introduction

Historical fire regimes in the forests of eastern Oregon and Washington varied with elevation and local topography. Low-severity, high-frequency fires were common in lower elevation, dry forest ecosystems through much of western North America prior to Euro-American settlement of the West (Arno et al., 1997; Everett et al., 2000; Hessburg and Agee, 2003). These fires reduced forest biomass primarily through low-intensity underburns and maintained an open forest structure (Covington and Moore, 1994). Conversely, wildfires tended to be less frequent but more often of stand-replacement intensity in higher elevation cool-moist and cold forest environments (Everett et al., 2000; Hessburg and Agee, 2003). Fire suppression, timber harvest,

and ungulate grazing have reduced wildfire frequency, increased conifer establishment, and changed the overall pattern and structure of forests of eastern Oregon and Washington (Hann et al., 1997; Hessburg et al., 2000). In particular, the area of old-forest and the number of remnant large- and medium-diameter trees ( $\geq 40$  cm diameter at breast height (dbh)) are currently a fraction of those present historically (Hessburg et al., 1999; Wisdom et al., 2000). Overall, current forests provide a much different mosaic of wildlife habitats than that of historical forests. Wisdom et al. (2000) found that habitats for more than 55 species of conservation concern in the interior Columbia River Basin have declined greatly since historical times (circa 1900). Of these, 21 species are closely associated with older coniferous forests, which showed the largest declines of all forest communities (Hann et al., 1997).

Throughout this paper, we refer to habitat as the macrovegetative structure and composition of primarily large-diameter coniferous forests in the interior northwestern United States, as described in detail by Wisdom et al. (2000). Numerous wildlife

\* Corresponding author. Tel.: +1 541 962 6535; fax: +1 541 962 6504.

E-mail addresses: [bwales@fs.fed.us](mailto:bwales@fs.fed.us) (B.C. Wales), [lsuring@fs.fed.us](mailto:lsuring@fs.fed.us) (L.H. Suring), [mhemstrom@fs.fed.us](mailto:mhemstrom@fs.fed.us) (M.A. Hemstrom).

species of conservation concern are associated with these forests (e.g., American marten (*Martes americana*; Buskirk and Ruggiero, 1994), fisher (*Martes pennanti*; Powell, 1993), brown creeper (*Certhia americana*; Hejl et al., 2002), and white-headed woodpecker (*Picoides albolarvatus*; Garrett et al., 1996)).

Re-creating natural fire regimes and actively managing fuels have often been advocated to maintain biological diversity and reduce the risk of catastrophic wildfire in forests throughout the west (Allen et al., 2002; Marston et al., 2001; Stuart, 1998). Ecological restoration projects are being planned and implemented on millions of hectares across the West and generally include thinning forests through combinations of tree harvesting and prescribed fire. However, these projects will likely produce large-scale changes in wildlife habitat composition and structure, which may affect the persistence of associated wildlife species of conservation concern. Because of the time required to grow old forests with large trees, it is important to implement long-term strategies to provide for a continuing supply of old forests. Therefore, implementing an aggressive fuels treatment program and/or restoring a more natural fire regime to forests of the interior west will need to be carefully considered to ensure that the resulting changes in ecosystem function do not have unforeseen biological and social consequences.

Forest vegetation and landscape simulation models in use today are valuable for evaluating potential biological and social consequences of different management scenarios over both short and long timeframes. Forest vegetation models can incorporate varying levels of management, natural disturbance (e.g., fire, insects, and disease), and associated vegetation succession. This allows land managers to better analyze the myriad of goals, objectives, and values placed on the landscape and to explore the compatibility and interaction of natural disturbance, management activities, and wildlife habitat goals through time and across large landscapes. Such tools provide managers with resources that may help evaluate ecological and socio-economic trade-offs as they implement forest restoration projects.

Our objectives were to: (1) examine the potential changes in amount and structure of forests with large trees following implementation of an aggressive program of fire and fuel management; (2) compare those changes to forest conditions that did not include management activities (i.e., only natural disturbance) and a program of aggressive fire suppression without active fuel management; (3) determine if areas within reserves (i.e., old-growth and riparian areas) might provide a supply of larger trees through time in disturbance-prone environments; and (4) evaluate the capability of current management standards (Ruediger et al., 2000) to provide habitats necessary for Canada lynx (*Lynx canadensis*). Although this species is not strictly associated with forests of large trees, it is designated as threatened under the USA Endangered Species Act (ESA) (U.S. Fish and Wildlife Service, 2000) and is the basis of significant management issues within our study area. Our wildlife habitat analysis was part of a large multi-resource project, the Interior Northwest Landscape Analysis System (INLAS), which was designed to advance the development and application of integrated landscape models and apply simulation methods to measure the relative effects of forest

succession, disturbance, and management on multiple-resource goals (Barbour et al., 2004).

## 2. Methods

### 2.1. Study area

Our analysis was conducted on approximately 178,000 ha of the upper Grande Ronde River Basin on the eastern flank of the Blue Mountains, southwest of La Grande, Oregon, USA (Fig. 1). The topography is highly varied and complex, with numerous deeply dissected drainages. Elevation in the watershed ranges from 360 m to over 2100 m. The climate in this area is characterized by short, dry summers and long, cold winters. Annual precipitation ranges from 230–460 mm in lower areas to 430–2540 mm at higher elevations. The USDA Forest Service, Wallowa–Whitman National Forest, administers approximately 122,100 ha of the watershed. Most of the remaining land is private (53,550 ha), with smaller amounts of land owned and managed by the Confederated Tribes of the Umatilla Indian Reservation (1370 ha), Bureau of Land Management (480 ha), and the State of Oregon (885 ha). Private lands contain few residences and are primarily managed for timber and cattle resources. Vegetation ranges from xeric, bunchgrass communities at the lower elevations to mixed-conifer and subalpine fir forests on the flanks of the mountains. Fire and insect infestations are the most significant disturbance agents in the watershed (Agee, 1993; DellaSala et al., 1995). A number of wildfires have occurred over the last 10 years, burning about 16,000 ha (nearly 10% of the watershed) and a western spruce budworm (*Choristoneura occidentalis*) outbreak in the 1980s followed by an outbreak of bark beetles (*Dendroctonus* sp.) caused significant mortality throughout the study area over the last two decades.

#### 2.1.1. Characterizing current vegetation

Hemstrom et al. (2006) classified current vegetation composition and structure by using aerial photographs and field stand examination data developed primarily by the Wallowa–Whitman and Umatilla National Forests. Although they classified vegetation across the entire study area (regardless of ownership), in this analysis we report on only forested vegetation and do not include non-forested grasslands and shrublands. Current vegetation was defined by three attributes: potential vegetation group (PVG), cover type, and structural stage. Potential vegetation types describe what vegetation will grow on a specific site and are grouped on the basis of a similar general moisture or temperature environment (Johnson and Clausnitzer, 1992). Three forested PVGs were used in this analysis: warm-dry, cool-moist, and cold. Ten cover types were characterized by the most abundant species in the overstory. Sixteen structural stages were based on six classes of tree size and number of canopy layers. Canopy closure (total canopy cover) was classified into two classes (open and closed). In cold-moist and cold forest environments, open-canopy classes were those with <60% canopy closure, and closed-canopy classes were those with ≥60% canopy cover. Warm-dry forest environments typically support lower canopy densities. Consequently, we defined

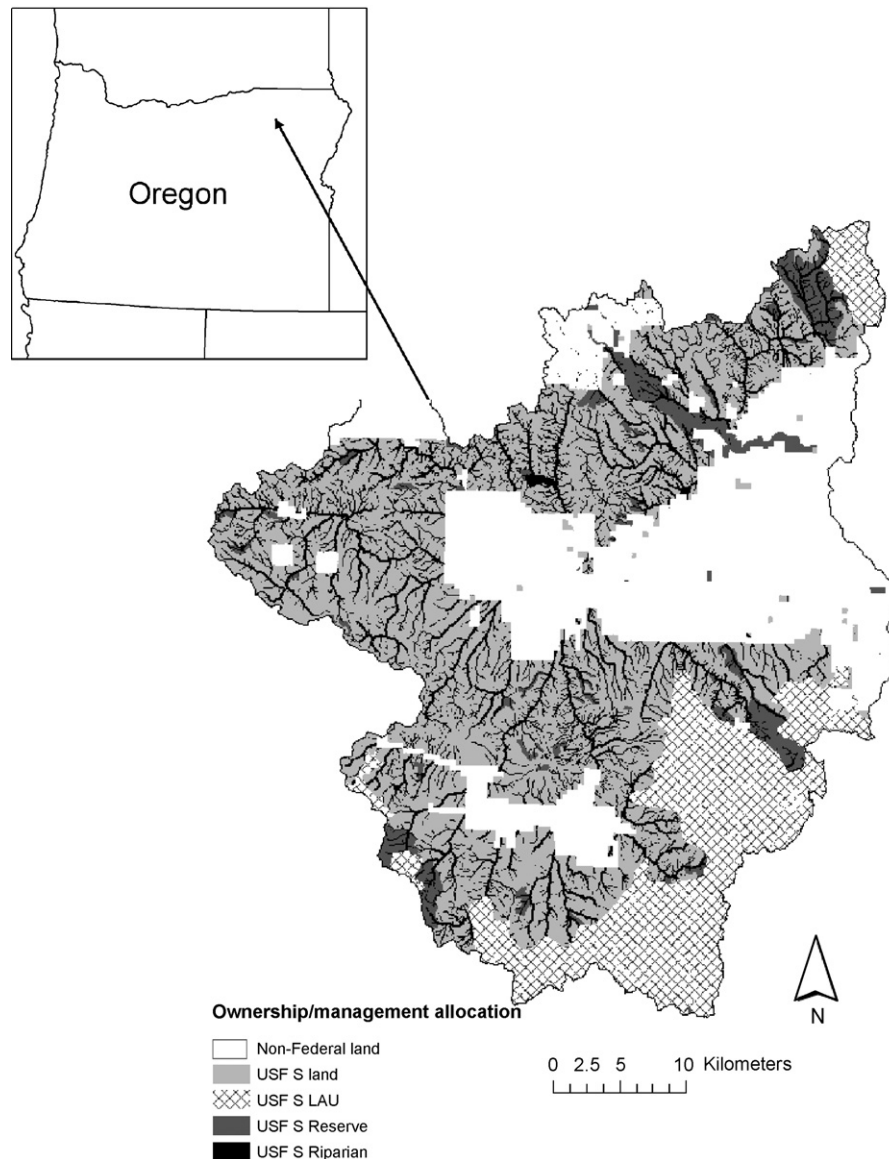


Fig. 1. Study area with land allocations in northeast Oregon, USA. Non-Federal lands do not have any special land management allocations. LAU is lynx analysis unit.

open-canopy habitats in warm-dry forests as those with  $<40\%$  canopy cover and closed-canopy habitats as those with  $\geq 40\%$  canopy cover. In total, to define current forested vegetation in the study area, 308 combinations of vegetation classes were described.

#### 2.1.2. Developing vegetation models

The Vegetation Development Dynamics Tool (VDDT; Beukema et al., 2003) was used to model vegetative composition and structure in response to both management treatments and natural disturbances (Hemstrom et al., 2006). VDDT is a non-spatial, transition probability model that links vegetation classes along multiple pathways of successional development and disturbance through time (e.g., Hemstrom et al., 2001; Kessell and Fischer, 1981). The current vegetation was classified into discrete states, and pathway diagrams were developed to portray succession between states. Disturbance probabilities for factors

such as wildfire (lethal, mixed severity, and non-lethal), mortality from insect and pathogen outbreaks in forests, wild ungulate grazing, domestic livestock grazing, and management activities (timber harvests, mechanical fuel treatments, prescribed burning) were defined from published research, local empirical data, and expert opinion (see Hemstrom et al., 2006, for more details).

#### 2.1.3. Establishing the natural range of variability in historical vegetation

A natural disturbance scenario (NAT\_DIST) was developed to emulate disturbance and succession patterns that were likely to have occurred prior to settlement of this area by Euro-Americans. Natural range of variability (NRV) is a concept that is based on the principle that ecosystems are naturally dynamic and that associated wildlife species have adapted to disturbance-driven changes in habitat conditions (Bunnell, 1995; Hunter,

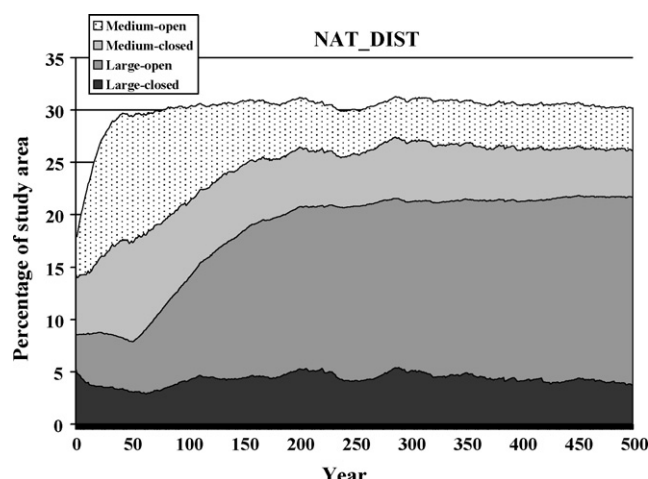


Fig. 2. Results of modeling vegetation under a natural disturbance regime in the study area. The average area of 30 Monte Carlo simulations at each time-step is displayed.

1991; Wimberly et al., 2000). We used the NAT\_DIST scenario to estimate natural disturbance and vegetation conditions that might exist if natural conditions were allowed to run their course without human interference under current climatic conditions. Our background NAT\_DIST scenario is similar to disturbance conditions assumed in various historical range of variability (HRV) analyses (Agee, 2003; Hann et al., 1997; Wimberly et al., 2000), but we do not assume that model projections actually represent some past set of conditions (Hemstrom et al., 2006). To calculate NRV, all silvicultural, fuel treatment, fire suppression, and non-native ungulate grazing activities were removed on all lands regardless of ownership (see Hemstrom et al., 2006, for additional information on modeling assumptions). The NAT\_DIST scenario was run for 500 years with 30 Monte Carlo simulations. We calculated the average and the high and low amounts of each particular vegetation state modeled from years 200 to 500 to describe the NRV. The years 200–500 were used because it was within this period that Hemstrom et al. (2006) found the area in various forest conditions became relatively constant or stable over time (Fig. 2). We used NRV

as a basis for our comparison of trends of different vegetation communities among management scenarios.

#### 2.1.4. Scenarios for modeling potential future vegetation

Four scenarios were developed to model potential vegetation conditions over the next 100 years: a scenario representing only background natural disturbance and three scenarios representing varying levels of management, including fire suppression (Table 1). The NAT\_DIST scenario emulated disturbance and succession patterns that are likely to occur if we were to take a hands-off approach without fire suppression or other management activities on all lands, regardless of ownership (Table 1). For this scenario, it was assumed that ungulate grazing (native and non-native) occurred at a rate that is lower than the current rate (see Vavra et al., 2006). The fire suppression only scenario (SUPPRESS) was developed to simulate forest succession with little active forest management except suppression of fires on Federal lands (Table 1). The only timber extraction activity on these lands under this scenario was salvage harvest of dead trees. On non-Federal lands, which include private, State and Tribal lands, we assumed active fuel treatment activities at rates similar to those currently implemented. In addition, grazing by non-native ungulates occurred at levels similar to current management in this scenario. Natural disturbance events caused by insects, diseases, and wildfires were set at current expected probabilities (Hemstrom et al., 2006).

Two active fuels management scenarios were developed to assist in displaying trade-offs associated with the current patchwork of regulatory policies applied across the landscape. The active fuels management (TREAT) scenario incorporated current land management allocations on Federal lands in the study area (Table 1). This scenario included limited active management in riparian habitat conservation areas (RHCAs) and Canada lynx conservation areas and no management in reserve allocations. Levels of fuel treatment activities on Federal and private lands reflected current levels.

To help evaluate the ecological trade-offs associated with constrained management in some areas on the landscape, a second active fuels management (TREAT\_ALL) scenario was developed. This scenario applied the same level of fuel treatment

Table 1  
A summary of the major assumptions and characteristics of each of the four modeling scenarios

Scenario	Land ownership	Fuels treatments in non-reserve allocations	Fuels treatments in reserve type allocations <sup>a</sup>	Salvage logging	Fire suppression	Grazing level
NAT_DIST	Public	No	No	No	No	Low
	Private	No	No	No	No	Low
SUPPRESS	Public	No	No	Yes	Yes	High
	Private	Yes	–	Yes	Yes	High
TREAT	Public	Yes	No/limited <sup>b</sup>	Yes	Yes	High
	Private	Yes	–	Yes	Yes	High
TREAT_ALL	Public	Yes	Yes	Yes	Yes	High
	Private	Yes	–	Yes	Yes	High

<sup>a</sup> Reserves in this table refer to land allocations of: riparian habitat conservation areas (RHCAs), lynx analysis units (LAUs), roadless areas, and old-growth management areas. Private lands do not have any reserve type land allocations.

<sup>b</sup> Under the TREAT scenario, very limited active fuels management can occur in RHCA's and LAU's.



as TREAT on all Federally-managed lands without regard to current land allocations. We wanted to assess the results of active fuel treatments without reserves established by the current land management plan (e.g., RHCAs, designated roadless areas, old-growth management areas, Canada lynx analysis units—LAUs) across the study area. Non-Federal lands do not have any of these reserve land allocations. In both of these active management scenarios, ungulate grazing (native and non-native) was assumed to occur at current levels, and natural disturbance patterns were set at current expected levels as described by Hemstrom et al. (2006).

## 2.2. Evaluating alternative management scenarios

### 2.2.1. Medium and large tree forests and canopy cover

We specifically focused on long-term projected trends in forests dominated by larger trees. Although medium (40–52.5 cm dbh) and large ( $\geq 52.5$  cm dbh) trees were included as different states in the vegetation model, we often combined these structure classes. Our review of the literature concerning habitat relationships for 202 wildlife species of conservation concern in eastern Oregon and Washington indicated that few species were highly associated only with large tree forests, although several species are highly associated with both medium and large trees. Owing to the concern, however, with the loss of large trees throughout the West (Allen et al., 2002; Brown et al., 2004), we felt it important to track them separately for some analyses. In addition, we found few species documented that specifically selected habitats based on the number of canopy layers in a forest so we combined multi- and single-story structures for our analyses. However, canopy closure was documented as an important characteristic in defining suitable habitat for species associated with these medium and large tree forests.

Except when we analyzed the effects of specific Federal land allocations (i.e., old-growth, RHCAs, LAUs), we considered all forested land within the study area for our evaluation. For our analysis of the Federal reserve allocations, we included only the vegetation within those particular areas. We did not include reference to mean NRV conditions in our discussion of vegetation response to management scenarios in riparian areas. Riparian areas are often quite different from adjacent uplands in composition and structure of vegetation, geomorphology, hydrology, microclimate, and fuel characteristics and as a result may differ in the frequency, severity, behavior, and extent of fire (Dwire and Kauffman, 2003). However, the probabilities for different disturbance or successional transitions in riparian areas were not different than the probabilities for upland forests in the vegetation model we used. Mean NRV, as calculated and applied in this analysis, was at the watershed scale and represented disturbances at that scale, not the finer-scale riparian management areas.

### 2.2.2. Canada lynx habitat assessment

In 2000, the Canada lynx was listed under the ESA as threatened in the United States. Under the provisions of the ESA, actions carried out by Federal agencies must not jeopardize the continued existence of any threatened or endangered species

or result in the destruction or adverse modification of critical habitat (16 USC 1536). To facilitate this directive, the USDA Forest Service (Forest Service), USDI Bureau of Land Management, and the USDI Fish and Wildlife (USFWS) collaborated to develop the Canada lynx conservation assessment and strategy (LCAS) (Ruediger et al., 2000). After completion of the LCAS, the Forest Service developed a Conservation Agreement with the USFWS that follows the recommendations of the LCAS. As one of the provisions of the LCAS, the Forest Service was required to develop Canada lynx LAUs, identify Canada lynx habitat within them, and implement the conservation measures in the LCAS. The Wallowa–Whitman National Forest designated 24,840 ha within the study area as LAUs. We analyzed how habitat for Canada lynx within these LAUs may change through time under each of the management scenarios.

The LCAS suggests that foraging and denning habitat be identified and managed for continued suitability as habitat for Canada lynx. Numerous authors have described Canada lynx habitat as mesic coniferous forests in a variety of forest ages and structural stages (Aubry et al., 2000). The primary prey species of Canada lynx are snowshoe hares (*Lepus americanus*), comprising 35–97% of the diet (Koehler and Aubry, 1994). Snowshoe hare population density is positively correlated with density of vegetation cover that is 1–3 m tall (Hodges, 2000). This dense, low cover can be provided by relatively young forested stands that have a substantial understory of conifers or with small patches of shrubs and young trees (Murray et al., 1994). Additionally, multi-storied mature conifer forests where low limbs provide cover at ground/snow level are also important to Canada lynx, particularly in winter (Parker et al., 1983; Murray et al., 1994). Red squirrels (*Tamiasciurus hudsonicus*) are the most important alternate prey species for Canada lynx, especially in years of low snowshoe hare abundance (Apps, 2000; Brand et al., 1976; O'Donoghue et al., 1998). Red squirrel abundance has been shown to be positively associated with older, closed-canopy forests with substantial quantities of coarse woody debris (Layne, 1954; Obbard, 1987; Klenner and Krebs, 1991 cited in the LCAS). Lynx denning habitat is described as areas with large woody debris, either down logs or root wads, within older regenerating stands or in mature conifer or mixed conifer-deciduous forests (Koehler, 1990; Mowat et al., 2000; Slough, 1999; Squires and Laurion, 2000).

Although we realize that under some conditions denning and foraging habitat characteristics may overlap, we grouped suitable habitats into foraging and denning habitat. We defined foraging habitat as those cover types and structural stages that consisted of either closed-canopy early successional forests or medium- or large-diameter, open-canopy multi-layered forests that we assumed would contain low cover either from small conifers or shrubs. We defined denning habitat as those cover types and structural stages that consisted of either closed-canopy of medium- and large-diameter forests, or areas of small- or medium-diameter forests that have gone through a natural disturbance event (e.g., wildfire, insect outbreak). Red squirrel habitat probably better corresponds to denning habitat as we have defined it rather than our definition of foraging habitat.

### 3. Results

#### 3.1. Trends in medium and large tree forests by canopy cover class

Natural disturbance patterns (simulation years 200–500, NRV) suggest that the open- and closed-canopy forests of large-diameter trees together would occupy about 20% of the area in this subbasin (Fig. 2). Currently, these forests represent <10% of the area as indicated by results corresponding to year 0 in Fig. 2. Interestingly, current areas of both medium and large tree closed-canopy forests and medium tree open-canopy forests are all close to the projected NRV, yet only 3% of the area is currently in large tree forests with open-canopy while the long-term average is about 17%.

All scenarios produced a slight decline in the percentage of the study area with large tree forests, and this trend continued for about 50 years (Fig. 3a–d). Without active fuels management activities, both the NAT\_DIST and SUPPRESS scenarios generated similar and fairly steady trends in closed-canopy large tree forests (Fig. 3a and b). The active fire and fuels management scenario (TREAT) projected a loss in area of closed-canopy large tree forests for 50 years, after which the area in these forests remained constant, well below the NRV (Figs. 2 and 3c). Similar management without reserves (TREAT\_ALL) led to a continual decline through year 100, with minimal area remaining in these closed-canopy forest conditions (Fig. 3d).

Under long-term stable conditions, the area in large tree forests with open canopies probably occupied about five times the current area (Fig. 2). However, model results suggest that it may take much longer than 100 years to restore this amount of open-canopy large tree forests in any scenario (Fig. 3a–d). The SUPPRESS scenario projected a decrease in area of open-canopy large tree forests compared to current conditions, owing to loss from natural disturbances and canopy closure following ingrowth. Conversely, the area in this forest class increased, with very similar patterns, over 100 years under the TREAT and TREAT\_ALL scenarios. After 50 years, the NAT\_DIST scenario generated a large increasing trend in open-canopy large tree forests and after 100 years, more than doubled in area.

The area in closed-canopy medium-diameter forests is currently (~4%) slightly above NRV levels (~3%) across the subbasin (Fig. 2). Area in this forest type continued to increase for about 50 years under the NAT\_DIST and SUPPRESS scenarios, nearly doubling, and then slowly decreased as trees grew to the large size class (Fig. 3a and b). The area in closed-canopy medium tree forests declined steadily over 100 years in the TREAT and the TREAT\_ALL scenarios to about 50 and 18% of the average NRV levels, respectively (Fig. 3c and d).

Area in open-canopy medium tree forests increased initially for all scenarios owing to management activities and natural disturbances (Fig. 3a–d). The area in these forests continued to increase in NAT\_DIST, TREAT, and TREAT\_ALL scenarios eventually exceeding the NRV by over 200%. In the NAT\_DIST scenario, an eventual decline is apparent as the trees grow into

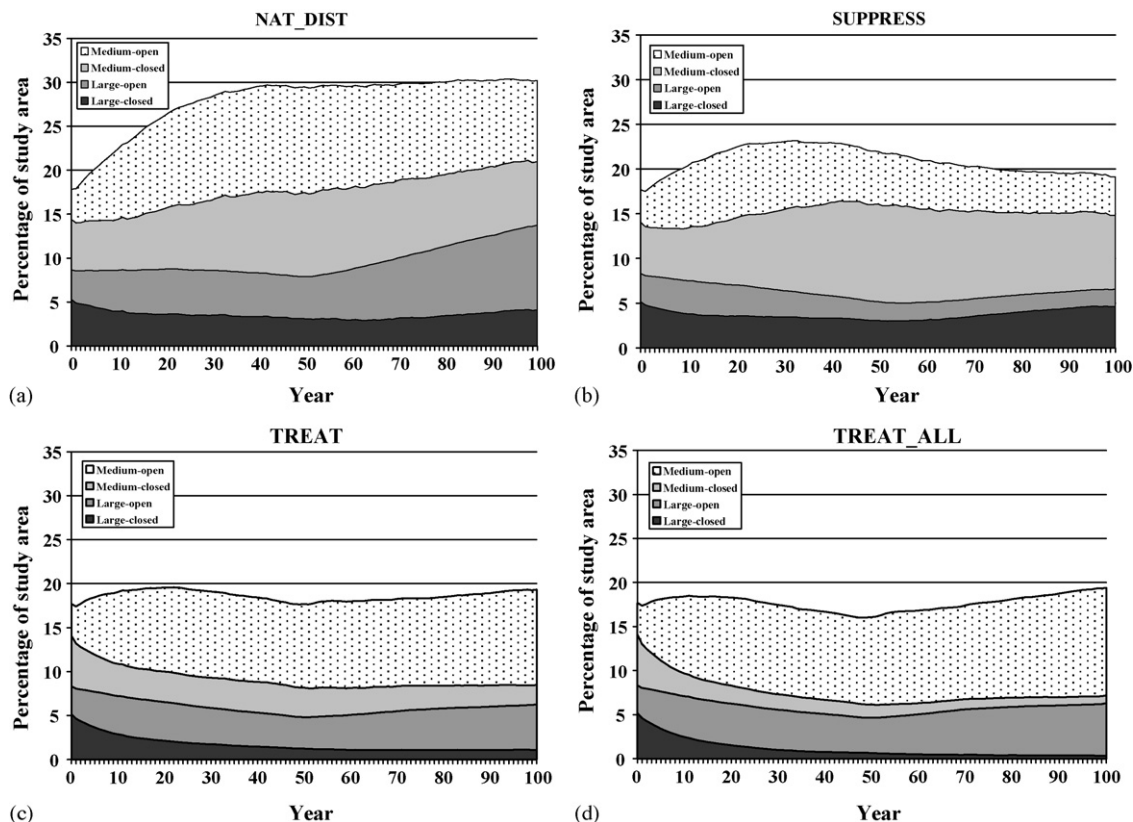


Fig. 3. Area of large ( $\geq 55$  cm dbh) and medium ( $\geq 40$  to  $< 55$  cm dbh) tree forests by management scenario in the study area: (a) NAT\_DIST, (b) SUPPRESS, (c) TREAT, and (d) TREAT\_ALL.

the large size class. The area in this class in the SUPPRESS scenario showed an increasing trend after about 30 years, ultimately returning to NRV levels owing to a natural closing of the canopy.

### 3.2. Trends in medium and large tree forests by potential vegetation type

Trends in the area of forests with larger trees differed greatly by PVG. The current area of medium and large tree forests in the warm-dry PVG is less than 50% of the NRV condition (Fig. 4a). In addition, the current proportions of open- and closed-canopy forests are opposite of those predicted under the long-term stable conditions (Fig. 4b and c). In fact, closed-canopy forests of medium and large tree forests are about double the NRV levels, while open-canopy forests are about one-tenth of the NRV. The area in medium and large tree closed-canopy forests in warm-dry environments decreased in all three scenarios over the first decade. These structural classes were nearly eliminated under the TREAT\_ALL scenario after about 40 years while limited area remained in the TREAT scenario. In contrast, the SUPPRESS scenario retained much of the current area in closed-canopy medium and large tree forests, and remained well above the NRV. However, the NAT\_DIST scenario eventually best emulated the NRV after several decades. Although currently well below the NRV, area in open-canopy medium and large tree forests immediately showed increasing trends in all scenarios. The area in these open habitats greatly increased, under the TREAT, TREAT\_ALL, and especially the NAT\_DIST scenario. However, it would take more than 100 years to reach the NRV. Throughout the 100-year simulation, the SUPPRESS scenario maintained approximately double the current area in this forest class though amounts remained well below the NRV.

Unlike the warm-dry PVG, the current area of medium and large forests in the cool-moist PVG is above the NRV (Fig. 5a). In this PVG, under the NAT\_DIST and SUPPRESS scenarios, area of closed-canopy medium and large tree forests increased through year 50 and then generated slower declines, with the SUPPRESS scenario showing areas of this class within the NRV throughout much of the 100-year simulation (Fig. 5b). However, area in these closed-canopy forests declined well below the NRV under the TREAT and TREAT\_ALL scenarios, with the greatest departure under the TREAT\_ALL scenario. In contrast, areas in open-canopy medium and large tree forests, currently well above the NRV (Fig. 5c), increased over the short term then steadily declined under all scenarios. The largest decrease was projected under the SUPPRESS scenario for this open-canopy class where levels approached mean NRV conditions after about 90 years.

The total area of medium and large tree forests in the cold PVG is below the NRV, as is the area with closed canopies (Fig. 6a and b). Both the TREAT and TREAT\_ALL management scenarios led to even further departures from the NRV, whereas the NAT\_DIST and SUPPRESS scenarios produced increases to within the NRV after about 40 years. Although representing only 5% of this PVG, the area of open-canopy medium and large tree forests, is currently above the NRV (Fig. 6c). After initial increases in all scenarios, the area of these open-canopy forests ultimately declined approaching the NRV after several decades.

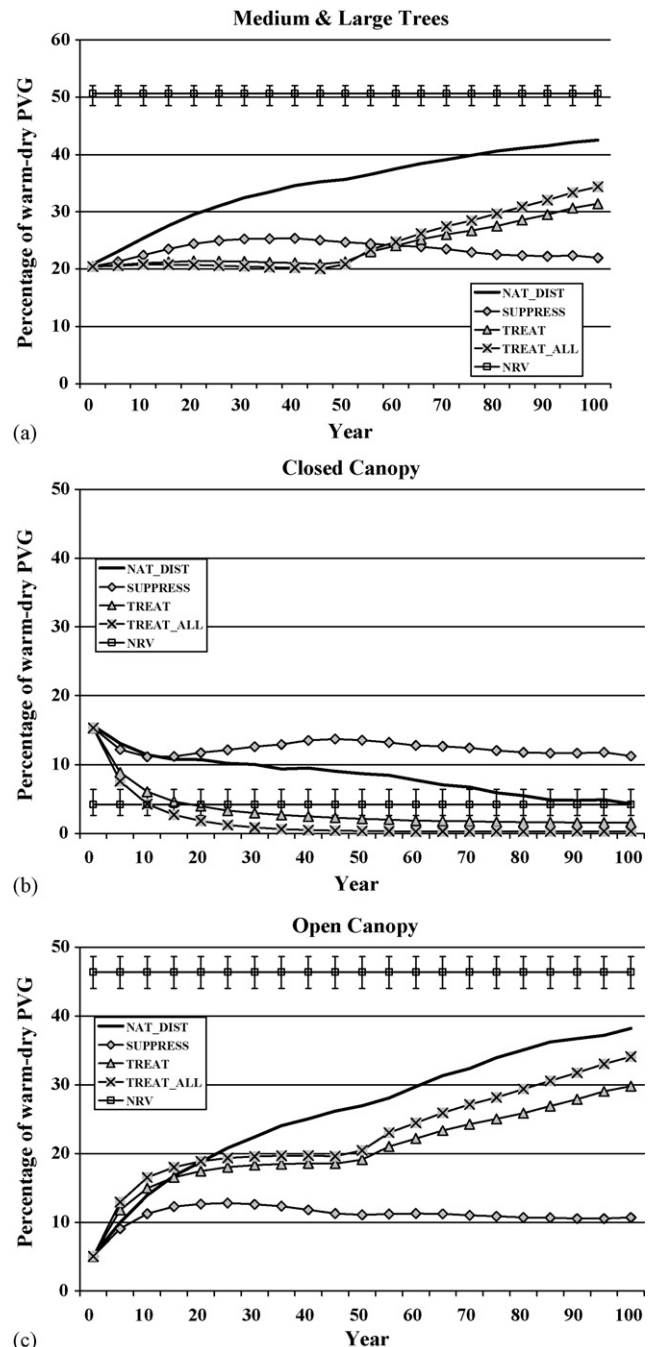


Fig. 4. Area of medium and large tree forests ( $\geq 40$  cm dbh) by: (a) total area, (b) closed-canopy, and (c) open-canopy in the warm-dry potential vegetation group (PVG) in the study area by management scenario. Natural range of variability (NRV) is represented by the average, high, and low amounts of each overstory structure state modeled under a natural disturbance regime from years 200 through 500 (see Fig. 2).

### 3.3. Trends in medium and large tree forests in reserves and RHCA's

Federally managed lands that have a reserved allocation (primarily roadless and designated old-growth areas) are under strict policy standards that limit management activities. These reserves comprise 4% of the study area, and currently 22% of their area is in medium and large tree forests (Fig. 7a), slightly



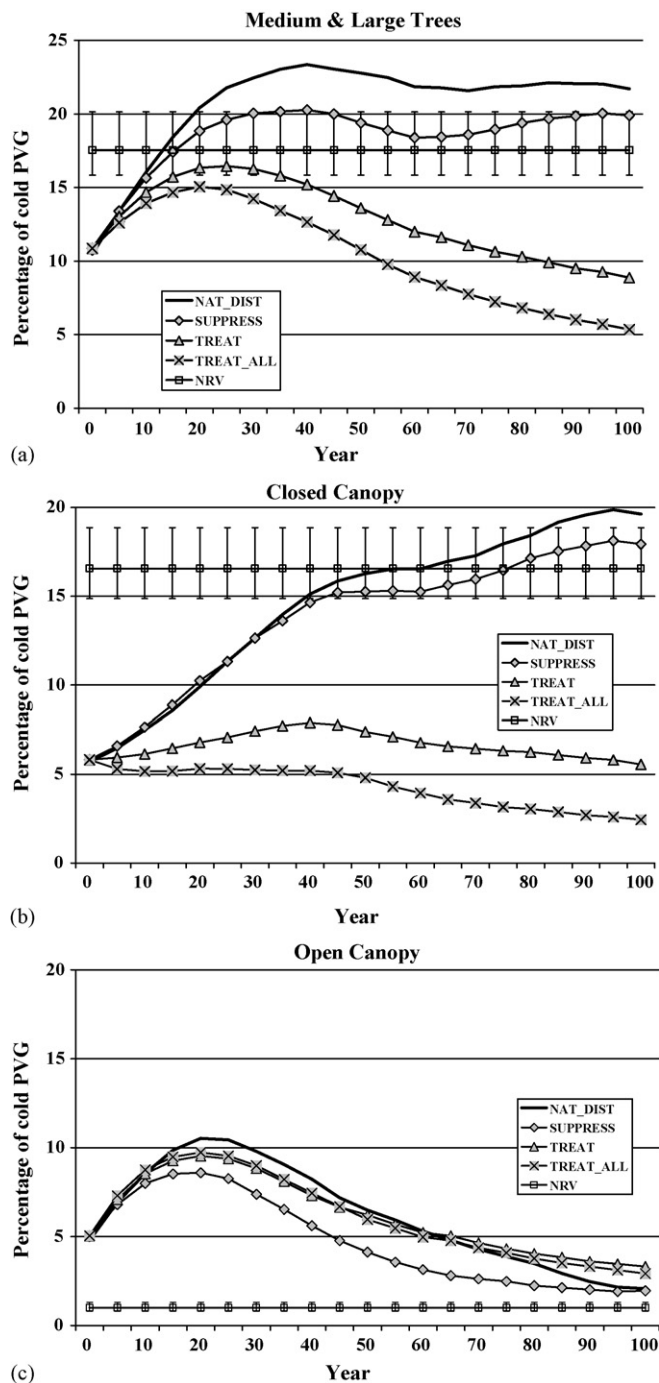
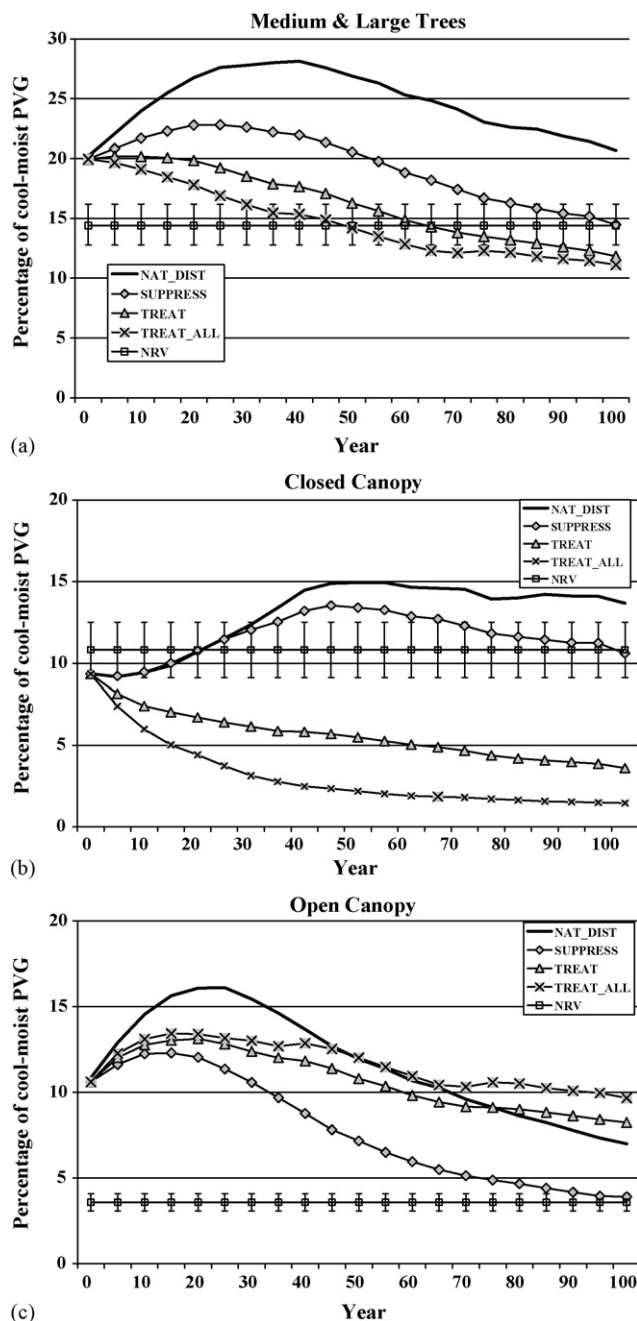


Fig. 5. Area of medium and large tree forests ( $\geq 40$  cm dbh) by: (a) total area, (b) closed-canopy, and (c) open-canopy in the cool-moist potential vegetation group (PVG) in the study area by management scenario. Natural range of variability (NRV) is represented by the average, high, and low amounts of each overstory structure state modeled under a natural disturbance regime from years 200 through 500 (see Fig. 2).

Fig. 6. Area of medium and large tree forests ( $\geq 40$  cm dbh) by: (a) total area, (b) closed-canopy, and (c) open-canopy in the cold potential vegetation group (PVG) in the study area by management scenario. Natural range of variability (NRV) is represented by the average, high, and low amounts of each overstory structure state modeled under a natural disturbance regime from years 200 through 500 (see Fig. 2).

higher than the 17% area across all allocations (Fig. 2). Although overall trends in the area of medium and large tree forests in reserves increased in all scenarios, the trends in open and closed-canopy conditions differed substantially by scenario (Fig. 7a–c). In the only scenario that allowed fuel treatments in reserves, the TREAT\_ALL, a drop in the area of closed-canopy medium and large tree forests below current levels and the NRV was predicted. After only 10 years under this scenario, the area of closed-canopy medium and large tree forests had declined to

50% of NRV levels. All other scenarios produced an increasing trend in the area in these forests for about 50 years and then a steady decline, though levels remained above current amounts and the NRV levels after 100 years.

Open-canopy medium and large tree forests in reserves are currently below the NRV (Fig. 7c). After 20 years under the TREAT\_ALL scenario, the area in open-canopy medium and



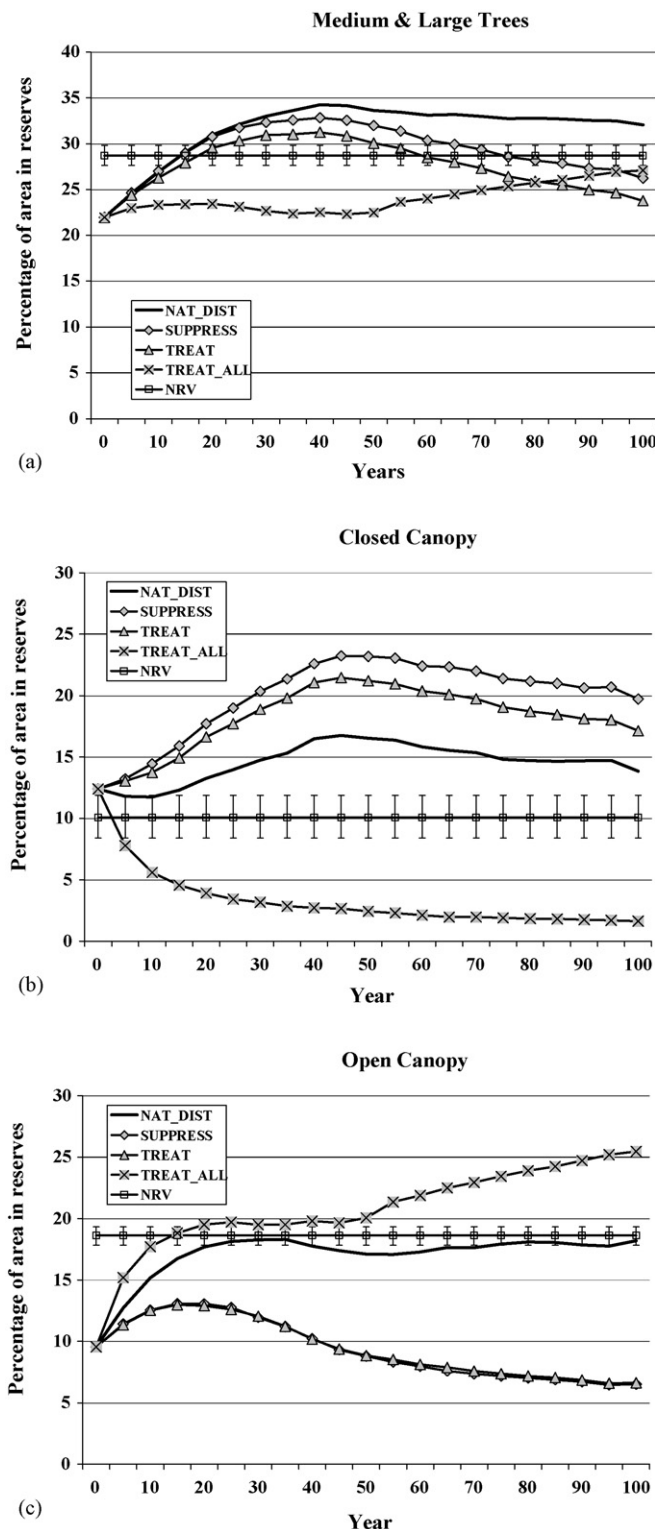


Fig. 7. Area of medium and large tree forests ( $\geq 40$  cm dbh) by: (a) total area, (b) closed-canopy, and (c) open-canopy in the reserve land allocation on Federal lands in the study area by management scenario. Natural range of variability (NRV) represented by the average, high, and low amounts of each overstory structure state modeled under a natural disturbance regime from years 200 through 500 (see Fig. 2).

large tree forests nearly doubled from current conditions toward mean NRV levels, and continued to increase above this level through 100 years. In contrast, both the SUPPRESS and TREAT scenarios generated similar downward trends. Similar trends in these scenarios would be expected because fire suppression is the only management activity occurring in the reserves in both scenarios. One hundred years of fire suppression and conifer establishment reduced areas in open-canopy medium and large tree forests to about 35% of the NRV. The NAT\_DIST scenario projected trends most similar to the NRV of these forests in reserves.

Riparian habitat conservation areas made up about 14% of the study area and about 15% of this is currently in medium and large tree forests. In RHCAs, very limited treatment was allowed under the TREAT scenario, whereas in the TREAT\_ALL scenario, treatment levels were much higher. Similar to reserves, area in medium and large tree forests increased in all scenarios, although the TREAT\_ALL scenario projected a slower increase over the first 50 years owing to more harvesting activities (Fig. 8a). The TREAT\_ALL scenario produced a strong decline in the area of closed-canopy medium and large tree forests that were ultimately 85% below current level (Fig. 8b). Areas in these classes of closed-canopy forests under the TREAT scenario remained similar to the current conditions, whereas both the NAT\_DIST and SUPPRESS scenarios projected increasing trends owing to natural filling in of the canopy. In particular, the SUPPRESS scenario showed nearly double the current amounts over 100 years.

Open-canopy, medium and large tree forests within RHCAs increased in all scenarios for the first 20 years (Fig. 7c). The TREAT\_ALL scenario was particularly effective in generating open-canopy forests, nearly doubling the area after just 7 years, whereas both the NAT\_DIST and TREAT scenarios also projected increasing trends. The SUPPRESS scenario projected long-term declines in area of these open-canopy forests and resulted in a return to current levels after about 80 years.

### 3.4. Canada lynx habitat assessment

As expected, different management scenarios within the LAUs produced differing levels of potential Canada lynx habitat. Foraging habitat increased from the current level under all scenarios except under the TREAT\_ALL scenario (Fig. 9a). The increase in mechanical fuel treatments in the TREAT\_ALL scenario led to an increase in the area of open seedling/sapling conditions that are not suitable foraging habitat.

All management scenarios led to a substantial loss of denning habitat within the LAUs through time (Fig. 9b). The NAT\_DIST and SUPPRESS scenarios resulted in declines of about 50% compared to current conditions, yet levels were projected to remain above the NRV. Both the active fuel treatment scenarios led to large declines in denning habitat over 100 years (Fig. 9b). In addition, the projected area of denning habitat declined to  $<10\%$  of the total area in the LAU after about 40 years under the TREAT\_ALL scenario, and in 65 years under the TREAT scenario. The Canada lynx assessment and conservation strategy recommends that denning habitat be present in at least 10% of

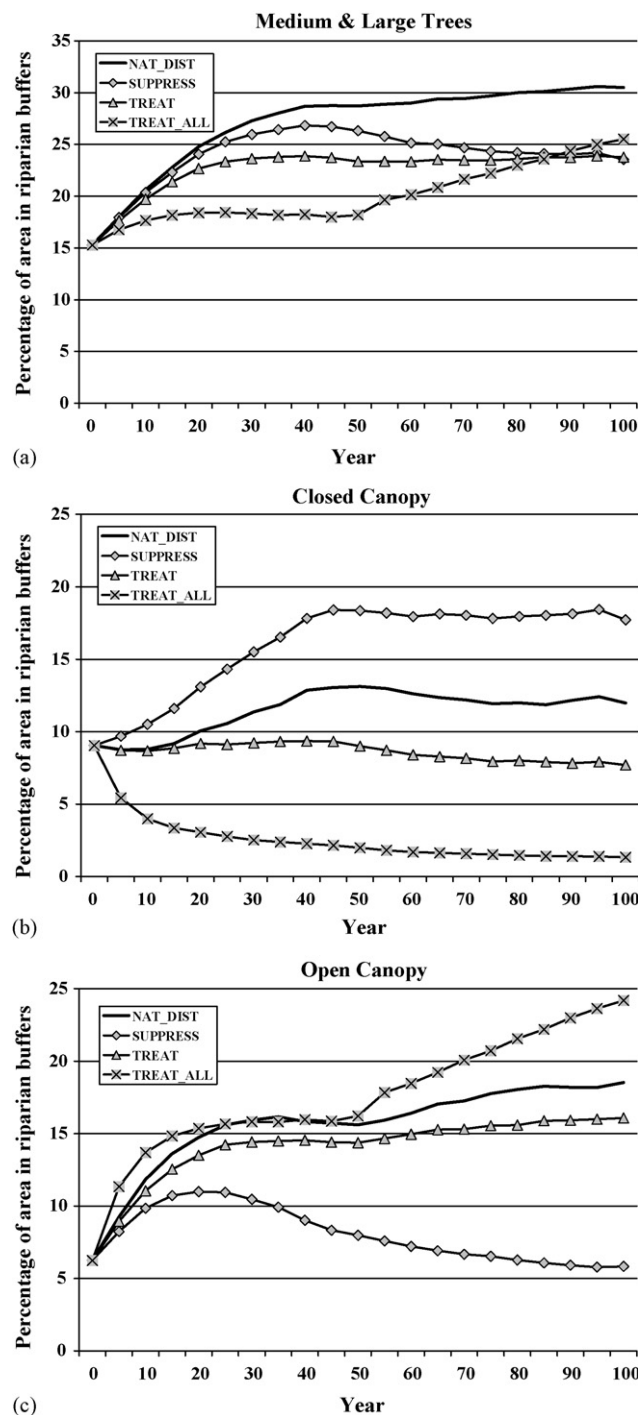


Fig. 8. Area of medium and large tree forests ( $\geq 40$  cm dbh) by: (a) total area, (b) closed-canopy, and (c) open-canopy in the riparian land allocation on Federal lands in the study area by management scenario.

the LAU, whereas our projections of the NRV has a mean of about 16%.

## 4. Discussion

### 4.1. Vegetation structure

Ecosystem management is concerned with the general goal of restoring and sustaining ecological integrity (Grumbine, 1993).

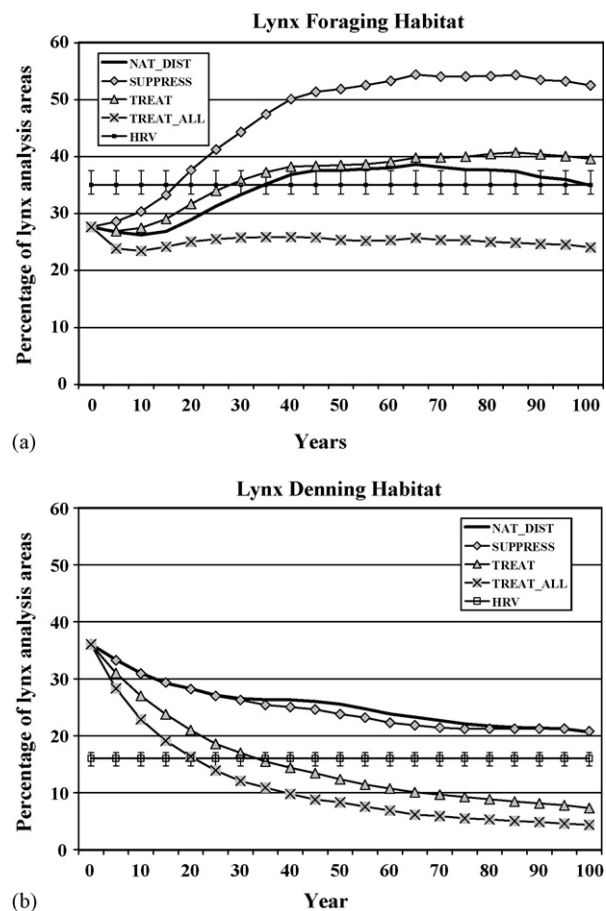


Fig. 9. Area of: (a) foraging and (b) denning habitat for Canada lynx in the study area by management scenario. Natural range of variability (NRV) is represented by the average, high, and low amounts of each overstory structure state modeled under a natural disturbance regime from years 200 through 500 (see Fig. 2).

Achieving ecosystem management goals on large forested landscapes will require strategies that provide a constant supply of older forests for wildlife habitat. This is especially important because such forest structures can be rapidly impacted by management activities and natural disturbances and may require decades or longer to restore.

Our projections of the NRV for the study area fall generally within estimated amounts of old forest types for other areas in the interior Pacific Northwest, with some exceptions. Overall our models indicate that about 30% of the study area might be in medium and large tree forests under natural conditions, including about 20% in the large-diameter class. Hessburg et al. (1999) estimated old-forest structural stages, similar to our large tree forests, to have occupied about 8% of the forested landscape in the Blue Mountains of Oregon. Our estimate that about 50% of the area in dry forest types might be in medium and large trees under natural conditions lies within the range of Agee's (2003) estimates for the ponderosa pine (*Pinus ponderosa*) zone (44–72%). Conversely, our estimates of medium and large tree forests in the higher elevation, cooler forests (about 15%) differ considerably from estimates made by Hessburg and Agee (2003) for similar forest types in eastern-side Washington Cascade forests (38–64%). However, Camp et al. (1997)

estimated about 12% late-successional and old structure in cold and moist forests in east-side Cascade forests in Washington but did not include the size of trees in their classification. Differences among these studies in definitions of large tree or old forest conditions, estimation methods, and local environments and disturbance regimes may account for some of the variability in results.

Our analysis of the area in medium and large tree forests by PVG clearly indicates that more closed-canopy medium and large tree habitat currently exists in warm-dry forests than in our estimated NRV (Fig. 4a). Conversely, more open-canopy forests currently exist in cool-moist and cold forests than in our NRV condition. Our active fuels management scenarios reduced levels of closed-canopy medium and large tree forests that provide important habitat for many species of conservation concern well below the NRV in all forest environments, but generated relatively high amounts of open-canopy medium and large tree forests. The NAT\_DIST scenario generated the highest amounts of all types of medium and large tree forests combined. The fire suppression only scenario produced relatively high levels of closed-canopy medium and large tree forests, but levels of severe wildfire and stand-replacing insect events were also high in the longer-term (Hemstrom et al., 2006). These results indicate several interesting possibilities regarding management for medium and large tree forests as wildlife habitat in the study area:

1. Active management approaches that focus on increasing open-canopy medium and large tree stands could overshoot NRV levels if not carefully planned.
2. Because wildlife habitat of large-diameter trees takes a long time to develop, extra efforts to conserve existing large tree forests in the short term may be needed as continued loss may occur due to harvest on private lands, wildfire, and insect activity.
3. The NRV for this landscape apparently does not support high levels of closed-canopy medium and large tree forests. Management direction to maintain these habitats should take this into consideration; objectives may be established to manage for more of this forest type than could be easily sustained. Wildfire and insects both play strong roles in determining sustainable levels of closed-canopy medium and large tree forests.
4. The probability of stand-replacing disturbance across the landscape makes the establishment of conservation strategies for closed-canopy medium and large tree forests very important. We suggest that designated reserves might be difficult to maintain in these conditions and that conservation might be more effective by using a landscape-wide approach that plans for the continual loss (through natural disturbance) and replacement (through growth and development) of these forest types through time (e.g., Everett and Lehmkuhl, 1996; Everett et al., 1994). Active management, in the form of carefully thought-out fuel treatments, might be necessary to encourage the development of closed-canopy medium and large tree forests in topographically or otherwise protected areas (i.e., refugia) to reduce loss to stand-replacing disturbances.

#### 4.2. Land allocations

Within reserves or riparian areas, trends of medium and large tree forests in response to management activities are similar to those in other land allocations although the overall area in this structural condition does tend to be slightly higher (~5%) than for the entire watershed after 100 years (Figs. 3, 7 and 8). Increasing levels of active fuels management activities increased open-canopy larger tree forests and decreased closed-canopy forests, whereas the combined level of medium and large tree forests stayed close to the projected NRV. Because we did not include a spatial component in our modeling of the probabilities for different disturbances or successional transitions in riparian areas, our projections of the structural composition of riparian areas may be inaccurate. For example, Hessburg and Agee (2003) pointed out, these small reserves and riparian areas (Fig. 1) may be at increased risk to large-scale disturbances (e.g., wildfire) that originate on adjacent lands and, as a result increases in abundance of forests with medium- and large-sized trees may be lower than we projected.

Fire, insect infestations, extreme wind events, and disease outbreaks often create early successional stages exploited by snowshoe hares, which are the primary prey species for Canada lynx in portions of their range (Agee, 2000; Kilgore and Heinzelman, 1990; Veblen et al., 1998). Our models suggest that fuel treatments and natural disturbance processes may produce suitable snowshoe hare habitat as potential foraging areas for Canada lynx. Several studies in the southern portion of Canada lynx range (Apps, 2000; Koehler, 1990; Squires and Laurion, 2000) have documented starvation as a primary cause of adult lynx mortality, as well as low kitten survival indicating that foraging habitat may be a limiting factor. If our projections of foraging habitat are correct, active fuels management will provide an abundance of snowshoe hare habitat. However, it has also been reported that in the southern part of the range of Canada lynx, there may be an increased reliance on other prey species, such as red squirrels (Apps, 2000; Koehler, 1990). We noted earlier that habitat for red squirrels is probably better represented in our designation of denning habitat for which we projected long-term declines. Denning habitat (i.e., closed-canopy forests of medium and large trees) will likely be limited in the study area without strategic planning.

It is important to realize the implications and limitations of our non-spatial analysis. Habitat use by Canada lynx, as well as other species, is known to be influenced by landscape attributes such as the amount of edge habitat, interior habitat, and patch size that we did not address in our modeling approach. Our approach was to model broad-scale trends in macro attributes of the composition and structure of forested habitats and should not be used to interpret potential population levels for individual species. By using a comprehensive vegetation model that included succession, natural disturbance, and varying levels of ungulate grazing and forest management activities, we were able to evaluate some of the potential trade-offs on broad-scale habitat conditions important for numerous upland vertebrates associated with medium and large tree forests of the inland northwest.



## 5. Conclusions

Our analysis indicated that the amount and type of large tree forests in the upper Grande Ronde River Basin have changed considerably from historical conditions when compared to natural disturbance conditions (Fig. 2) and might vary considerably into the future depending on management approach (Fig. 3). None of our scenarios produced areas of large-diameter forests approaching NRV in 100 years, highlighting the importance of existing trees that are, or soon might become,  $\geq 52.5$  cm in diameter.

It is apparent that specific management strategies will be necessary to maintain populations of all wildlife species. As Hessburg and Agee (2003) suggested, “Traditional reserve type networks may be susceptible to large-scale disturbances, perhaps we need to develop an approach that marries a short-term system of reserves with a long-term strategy to convert to a continuous network of landscapes with dynamic properties. In such a system, late-successional and old forest elements would be continuously recruited, but would shift semi-predictably in landscape position across space and time.”

Although we analyzed broad-scale changes in forest composition and structure, fine-scale habitat features also need to be considered to ensure high-quality, large-diameter trees as wildlife habitat through time. Attention should be given to protecting existing large-diameter and old trees (especially fire-resistant species) because they are difficult to replace (Allen et al., 2002; Brown et al., 2004; Henjum et al., 1994). In addition, the long-term abundance and replacement of large snags and down logs should be considered in light of fall down and decomposition rates throughout the landscape (Mellen et al., 2003). Prescribed fire can kill large trees that are intended to be retained and benefit from treatment (Agee, 2003), so it may be necessary to remove slash and fuels surrounding individual trees or logs to protect them.

Conservation of medium and large tree forests might require novel approaches and careful consideration of landscape potentials and sustainability. In particular, cold and moist closed-canopy forests of medium- and large-diameter trees warrant attention because they are highly susceptible to stand-replacing disturbance in this landscape and NRV levels are generally about 15% of the landscape area. Given these issues, we suggest landscape-wide management that fosters development of closed-canopy medium and large tree forests in topographically or otherwise protected areas and that takes into account the ephemeral nature of this forest structure. We anticipate that this approach might be more effective than traditional reserve designs.

## Acknowledgements

The authors would like to acknowledge support from the USDA Forest Service, PNW Research Station for project funding. We thank Jamie Barbour, Marty Raphael, Mike Wisdom, Kelly Burnett and two anonymous reviewers for helpful comments and suggestions on an earlier draft of this manuscript.

## References

- Agee, J.K., 1993. Fire Ecology of Pacific Northwest Forests. Island Press, Washington, DC.
- Agee, J.K., 2000. Disturbance ecology of North American boreal forests and associated northern mixed/subalpine forests. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), Ecology and Conservation of Lynx in the United States. University Press of Colorado, Boulder, CO, pp. 39–82.
- Agee, J.K., 2003. Historical range of variability in eastern Cascades forests, Washington, USA. *Landscape Ecol.* 18, 725–740.
- Allen, C.D., Savage, M., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M., Klingel, J.T., 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecol. Appl.* 12 (5), 1418–1433.
- Apps, C.D., 2000. Space-use, diet, demographics, and topographic associations of lynx in the southern Canadian Rocky Mountains: a study. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), Ecology and Conservation of Lynx in the United States. University Press of Colorado, Boulder, CO, pp. 351–371.
- Arno, S.F., Smith, H.Y., Krebs M.A., 1997. Old growth ponderosa pine and western larch stand structures: influences of pre-1900 fires and fire exclusion. Res. Pap. INT-RP-495. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.
- Aubry, K.B., Koehler, G.M., Squires, J.R., 2000. Ecology of Canada lynx in southern boreal forests. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), Ecology and Conservation of Lynx in the United States. University Press of Colorado, Boulder, CO, pp. 373–396.
- Barbour, R.J., Ager, A.A., Hayes, J.L., 2004. A framework for the development and application of INLAS: the interior northwest landscape analysis system. In: Hayes, J.L., Ager, A.A., Barbour, R.J. (Tech. Eds.), Methods for Integrating Modeling of Landscape Change: Interior Northwest Landscape Analysis System. Gen. Tech. Rep. PNW-GTR-610. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, pp. 1–16.
- Beukema, S.J., Kurz, W.A., Pinkham, C.B., Milosheva, K., Frid, L., 2003. Vegetation Dynamics Development Tool, User's Guide, Version 4.4c. ESSA Technologies Ltd., Vancouver, BC, Canada, 239 pp.
- Brand, C.J., Keith, L.B., Fischer, C.A., 1976. Lynx responses to changing snowshoe hare densities in Alberta. *J. Wildl. Manage.* 40, 416–428.
- Brown, R.T., Agee, J.K., Franklin, J.F., 2004. Forest restoration and fire: principles in the context of place. *Conserv. Biol.* 18, 903–912.
- Bunnell, F.L., 1995. Forest-dwelling vertebrate faunas and natural fire regimes in British Columbia: patterns and implications for conservation. *Conserv. Biol.* 9, 636–644.
- Buskirk, S.W., Ruggiero, L.F., 1994. The American marten. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Lyon, L.J., Zielinski, W.J. (Eds.), The Scientific Basis for Conserving Forest Carnivores: American Marten, Fisher, Lynx, and Wolverine in the Western United States. Gen. Tech. Rep. RM-254. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO, pp. 7–37.
- Camp, A., Oliver, C., Hessburg, P., Everett, R., 1997. Predicting late successional fire refugia pre-dating European settlement in the Wenatchee Mountains. *For. Ecol. Manage.* 95, 63–77.
- Covington, W.W., Moore, M.M., 1994. Southwestern ponderosa pine forest structure: changes since Euro-American settlement. *J. For.* 92, 39–47.
- DellaSala, D.A., Olson, D.M., Barth, S.E., Crane, S.L., Primm, S.A., 1995. Forest health—moving beyond rhetoric to restore healthy landscapes in the Inland Northwest. *Wildl. Soc. Bull.* 23, 346–356.
- Dwire, K.A., Kauffman, J.B., 2003. Fire and riparian ecosystems in landscapes of the western USA. *For. Ecol. Manage.* 178, 61–74.
- Everett, R.L., Hessburg, P.F., Lemkuhl, J., Jensen, M., Bourgeron, P., 1994. Old forests in dynamic landscapes. *J. For.* 92, 22–25.
- Everett, R.L., Lemkuhl, J.F., 1996. An emphasis—use approach to conserving biodiversity. *Wildl. Soc. Bull.* 24, 192–199.
- Everett, R.L., Schellhaas, R., Keenum, D., Spurbeck, D., Ohlson, P., 2000. Fire history in the ponderosa/Douglas-fir forests on the east slope of the Washington Cascades. *For. Ecol. Manage.* 129, 207–225.



- Garrett, K.L., Raphael, M.G., Dixon, R.D., 1996. White-headed woodpecker (*Picoides albolarvatus*). In: Poole, A., Gill, F. (Eds.), The Birds of North America, No. 252. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, DC.
- Grumbine, R.E., 1993. What is ecosystem management? *Conserv. Biol.* 8, 27–38.
- Hann, W.J., Jones, J.L., Karl, M.G., Hessburg, P.F., Keane, R.E., Long, D.G., Menakis, J.P., McNicoll, C.H., Leonard, S.G., Gravenmier, R.A., Smith, B.G., 1997. Landscape dynamics of the basin. In: Quigley, T.M., Arbelbide, S.J. (Tech. Eds.), An Assessment of Ecosystem Components in the Interior Columbia Basin and Portions of the Klamath and Great Basins. Gen. Tech. Rep. PNW-GTR-405, vol. 2. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, pp. 337–1055.
- Hejl, S.J., Newlon, K.R., McFadzen, M.E., Young, J.S., Ghalambor, C.K., 2002. Brown creeper (*Certhia americana*). In: Poole, A., Gill, F. (Eds.), The Birds of North America, No. 252. Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, DC.
- Hemstrom, M.A., Korol, J.J., Hann, W.J., 2001. Trends in terrestrial plant communities and landscape health indicate the effects of alternative management strategies in the interior Columbia River basin. *For. Ecol. Manage.* 153, 105–126.
- Hemstrom, M.A., Merzenich, J., Reger, A., Wales, B., 2006. Integrated analysis of landscape management scenarios using state and transition models in the upper Grande Ronde River Subbasin, Oregon, USA. *Landscape Urban Plan.*, doi:10.1016/j.landurbplan.2006.10.004.
- Henjum, M.G., Karr, J.R., Bottom, D.L., Perry, D.A., Bednarz, J.C., Wright, S.G., Beckwitt, S.A., Beckwitt, E., 1994. Interim protection for late-successional forests, fisheries, and watersheds: national forests east of the Cascades crest, Oregon and Washington. Technical Reviews 94-2. The Wildlife Society, Bethesda, MD.
- Hessburg, P.F., Agee, J.K., 2003. An environmental narrative of inland Northwest United States forests, 1800–2000. *For. Ecol. Manage.* 178, 23–59.
- Hessburg, P.F., Smith, B.G., Kreiter, S.G., Miller, C.A., Salter, R.B., McNicholl, C.H., Hann, W.J., 1999. Historical and current forest and range landscapes in the Interior Columbia River Basin and portions of the Klamath and Great Basins. Part 1. Linking vegetation patterns and landscape vulnerability to potential insect and pathogen disturbances. Gen. Tech. Rep. PNW-GTR-458. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, 357 pp.
- Hessburg, P.F., Smith, B.G., Salter, R.B., Ottmar, R.D., Alvarado, E., 2000. Recent changes (1930s–1990s) in spatial patterns of interior northwest forests, USA. *For. Ecol. Manage.* 136, 53–83.
- Hodges, K.E., 2000. Ecology of snowshoe hares in southern boreal and montane forests. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), Ecology and Conservation of Lynx in the United States. University Press of Colorado, Boulder, CO, pp. 163–206.
- Hunter Jr., M.L., 1991. Coping with ignorance: the coarse-filter strategy for maintaining biodiversity. In: Kohn, K.A. (Ed.), Balancing on the Brink of Extinction. Island Press, Washington, DC, pp. 266–281.
- Johnson, C.G., Jr., Clausnitzer, R.R., 1992. Plant associations of the Blue and Ochoco Mountains. R6-ERWT-036-92. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Portland, OR.
- Kessell, S.R., Fischer, W.C., 1981. Predicting post-fire plant succession for fire management planning. Gen. Tech. Rep. INT-GTR-94. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT.
- Kilgore, B.M., Heinselman, M.L., 1990. Fire in wilderness ecosystems. In: Hendee, J.C., Stankey, G.H., Lucas, R.C. (Eds.), Wilderness Management, second ed. North American Press, Golden, CO, pp. 297–335.
- Klenner, W., Krebs, C.J., 1991. Red squirrel population dynamics. I. The effect of supplemental food on demography. *J. Anim. Ecol.* 60, 961–978.
- Koehler, G.M., 1990. Population and habitat characteristics of lynx and snowshoe hares in north central Washington. *Can. J. Zool.* 68, 845–851.
- Koehler, G.M., Aubry, K.B., 1994. Lynx. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Lyon, L.J., Zielinski, W.J. (Eds.), The Scientific Basis for Conserving Forest Carnivores: American Marten, Fisher, Lynx, and Wolverine in the Western United States. Gen. Tech. Rep. RM-254. U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, CO, pp. 74–98.
- Layne, J.N., 1954. The biology of the red squirrel, *Tamiasciurus hudsonicus loquax* (Bangs), in central New York. *Ecol. Monogr.* 24, 227–267.
- Marston, E.L., Criley, A., Brower, S., Kennedy, J., Downing, H., Nolde, C., Smith, H., Swartz, H., 2001. “Restoring the range of light” [a series of articles]. *High Country News*, 27 August, pp. 1, 8–14.
- Mellen, K., Marcot, B.G., Ohmann, J.L., Wadell, K., Livingston, S.A., Wilhite, E.A., Hostetler, B.B., Ogden, C., Dreisbach, T., 2003. DecAID, the decayed wood advisor for managing snags, partially dead trees, and down wood for biodiversity in forests of Washington and Oregon, Version 1.10. U.S. Department of Agriculture, Forest Service, Pacific Northwest Region and Pacific Northwest Research Station, U.S. Department of the Interior, Fish and Wildlife Service, Oregon State Office, Portland, OR. <http://www.notes.fs.fed.us:81/pnw/DecAID/DecAID.nsf>.
- Mowat, G., Poole, K.G., O'Donoghue, M., 2000. Ecology of lynx in northern Canada and Alaska. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), Ecology and Conservation of Lynx in the United States. University Press of Colorado, Boulder, CO, pp. 265–306.
- Murray, D.L., Boutin, S., O'Donoghue, M., 1994. Winter habitat selection by lynx and coyotes in relation to snowshoe hare abundance. *Can. J. Zool.* 72, 1444–1451.
- O'Donoghue, M., Boutin, S., Krebs, C.J., Zuleta, G., Murray, D.L., Hofer, E.J., 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology* 79, 1193–1208.
- Obbard, M.E., 1987. Red squirrel. In: Novak, M., Baker, J.A., Obbard, M.E., Malloch, B. (Eds.), Wild Furbearer Management and Conservation in North America. Ontario Trappers Assoc., North Bay, Ontario, pp. 264–281.
- Parker, G.R., Maxwell, J.W., Morton, L.D., Smith, G.E.J., 1983. The ecology of the lynx (*Lynx canadensis*) on Cape Breton Island. *Can. J. Zool.* 61, 770–786.
- Powell, R.A., 1993. The Fisher: Life History, Ecology, and Behavior. University of Minnesota Press, MN.
- Ruediger, B., Claar, J., Gniadek, S., Holt, B., Lewis, L., Mighton, S., Naney, B., Patton, G., Rinaldi, T., Trick, J., Vandehey, A., Wahl, F., Warren, N., Wenger, D., Williamson, A., 2000. Canada Lynx Conservation Assessment and Strategy. U.S. Department of Agriculture, Forest Service, U.S. Department of the Interior, Fish and Wildlife Service, U.S. Department of the Interior, National Park Service, Missoula, MT.
- Slough, B.G., 1999. Characteristics of Canada lynx, *Lynx canadensis*, maternal dens and denning habitat. *Can. Field-Nat.* 113, 605–608.
- Squires, J.R., Laurion, T., 2000. Lynx home range and movements in Montana and Wyoming: preliminary results. In: Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S., Squires, J.R. (Eds.), Ecology and Conservation of Lynx in the United States. University Press of Colorado, Boulder, CO, pp. 337–349.
- Stuart, J.D., 1998. Effects of fire suppression on ecosystems and diversity. In: Mac, M.J., Opler, P.A., Puckett Haecker, C.E., Doran, P.D. (Eds.), Status and Trends of the Nation's Biological Resources, 2 vols. U.S. Department of the Interior, U.S. Geological Survey, Reston, VA, pp. 45–47.
- U.S. Fish and Wildlife Service, 2000. Endangered and threatened wildlife and plants, determination of threatened status for the contiguous U.S. distinct population segment of the Canada lynx and related rule, final rule. *Federal Register*. 65, 16052–16086.
- Vavra, M., Hemstrom, M.A., Wisdom, M., 2006. Modeling the effects of herbivores on the abundance of forest overstory states using a state-transition approach in the upper Grande Ronde River Basin, Oregon, USA. *Landscape Urban Plan.*, doi:10.1016/j.landurbplan.2006.10.005.
- Veblen, T.T., Hadley, K.S., Nel, E.M., Kitzberger, T., Reed, M., Villalba, R., 1998. Disturbance regimes and disturbance interactions in a Rocky Mountain subalpine forest. *J. Ecol.* 82, 125–135.

Wimberly, M.C., Spies, T.A., Long, C.J., Whitlock, C., 2000. Simulating historical variability in the amount of old forests in the Oregon Coast Range. *Conserv. Biol.* 14, 167–180.

Wisdom, M.J., Holthausen, R.S., Wales, B.C., Hargis, C.D., Saab, V.A., Lee, D.C., Hann, W.J., Rich, T.D., Rowland, M.M., Murphy, W.J., Eames, M.R.,

2000. Habitats for terrestrial vertebrates of focus in the interior Columbia Basin: broad-scale trends and management implications, 3 vols. Gen. Tech. Rep. PNW-GTR-485. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR.